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Marine Biological Laboratory

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BIOLOGICAL BULLETIN.

NOTES ON THE REGENERATION OF GONIONEMA.

G. T. HARGITT.

The experiments of which this paper presents a résumé were conducted at the Marine Biological Laboratory during the summer of 1901. The purpose in view was such a review of previous work done by C. W. Hargitt '97,[1] '99,[2] and by Morgan '99,[3] as would confirm or correct, or possibly extend, the conclusions then announced.

The work was suggested by and the experiments carried on under the direction of C. W. Hargitt, whose advice and oversight has been largely instrumental in making possible the preparation of this paper.

By way of introduction it may be stated that three general series of experiments were projected:

I. Experiments upon the regeneration of the marginal organs of the medusæ.

II. Experiments on the regeneration of the manubrium.

III. Experiments upon the regeneration of the radial canals.

Under each of these series several sets of experiments were conducted, and under each set a sufficient number of specimens operated upon to insure reasonable precautions against failure or unwarranted conclusions from limited observations. In other words the repeated experiments operated as controls or checks against exceptional results in either direction.

In general the methods followed were similar to those of previous experiments. The medusæ were operated upon very soon after being brought into the laboratory, being cut into desired forms by means of clean scissors as the animals were

[1] *Zoölogical Bulletin*, Vol. I., p. 27.
[2] BIOLOGICAL BULLETIN, Vol. I., p. 35.
[3] *The American Naturalist*, Vol. XXXIII., p. 939.

held gently, by means of delicate forceps, in dishes of perfectly fresh sea water. After the operation the specimens were immediately transferred to clean sea water, which was afterward changed at least daily and sometimes oftener. The specimens were fed from time to time with bits of freshly killed shrimp or small fish. The specimens usually seemed to thrive quite well considering the artificial conditions under which they were placed and the mutilation to which the operations had subjected them. Occasionally, as will be noted later, whole sets under a given experiment would seem to decline or go bad, a fact doubtless due to accidental contamination of the water in which they were kept.

I. Experiments upon the Regeneration of the Marginal Organs of the Medusæ.

Hargitt '97, and Morgan 99, found that when the entire margin was removed new tentacles regenerated though in their investigations they remained rudimentary and bud-like. I repeated experiments of a similar kind to see in how far my results would confirm theirs. Five sets of experiments were tried.

In all cases the cut edges contracted more or less. In the first set the contraction continued till the edges had nearly met and the bell was spherical and had only a very small opening into the subumbrella. Five days after the operation small refractile bulbs were found at the lower distal pole of the sphere, in several specimens. The next day tentacles had begun to grow from these bulbs. On the ninth day two to four tentacles were found on those in which the bulbs had earlier formed. These tentacles were of considerable length, had the rings of nematocysts and the suctorial pads found in the mature tentacles (Fig. 1). As the opening was so small as to prevent the taking of food, the specimens died before further developments could take place. Particular care was taken to remove the entire margin with all the tentacles and bulbs at the time of operation, so that these regenerated tentacles were undoubtedly of new growth.

In the second set the cut edges contracted, though not into a sphere, and a large opening into the subumbrella was left. No velum formed in any of the specimens. In two days several bulbs had formed on some of the margins. In four days marginal

canals and several bulbs had formed in other specimens. Quite a large number of bulbs were present; in some cases thirty were counted, while in others as many as forty were found. These bulbs are probably an aggregation of new tissue and do not represent the bulbs usually found at the bases of mature tentacles, as these latter normally form after the tentacles have been regenerated. In Fig. 2 the marginal canal and bulbs are shown. From several of the bulbs elongations resembling young tentacles had formed. Specimens were kept two weeks after the bulbs were first found and though the bulbs increased from two or three to twenty or forty the tentacles did not develop beyond what is shown in Fig. 2.

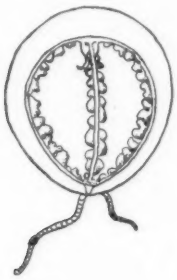

FIG. 1.

FIG. 2.

In the third set the margins contracted somewhat, but on the second day all evaginated and in some cases the bell began to degenerate. One of the specimens turned right side out and twelve hours later evaginated again and then gradually disintegrated. All the specimens died before any regeneration took place. In the fourth set all died within a week without having regenerated. One specimen flattened out and attached itself to the bottom of the dish by the manubrium. Several of them evaginated and in all the bell slowly disintegrated and the medusæ soon died.

The fact that in these two sets nearly all evaginated and all died within a week, and that this happened only in this experiment, needs some further explanation. The same care and methods were used in this experiment as in all others, with the exception that in the third set the water was taken from the tap

in the laboratory, while in most of the others it was taken directly from the open harbor. Since in these two sets the medusæ were placed in smaller dishes, the consequent overcrowding may have been the cause of their death, through lack of aëration.

In order to ascertain whether the regeneration of new tentacles would take place more rapidly if a portion of the margin was left, than when it was entirely removed, three quarters of the margin was excised leaving one quarter of the original number of tentacles still present. The part from which the tentacles had been removed gradually contracted till it occupied only about one quarter or one half of the new margin. Thus two or three canals were crowded into less than half of the margin and two of them sometimes fused as shown in Fig. 3. New marginal canals were fully formed in about a week, and the circulation of the fluid in them could be observed. In ten or twelve days small bulbs were found on the margins of some, and from these bulbs

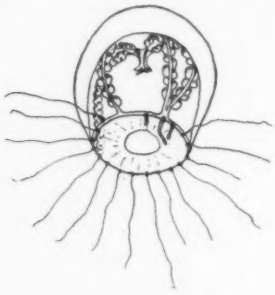

FIG. 3.

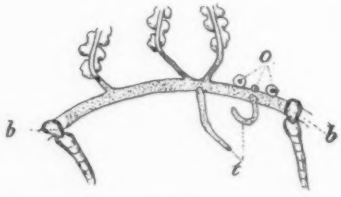

FIG. 4.

tentacles formed, while at about the same time new otocysts developed. As suggested under the second set these bulbs are probably aggregations of new tissue, and are perhaps comparable to the tentacle "anlagen" in regenerating hydroids. Fig. 4 shows the portion of the margin from which the tentacles were excised, *o* represents otocysts and *t* the new tentacles. It will be seen that the pads or bulbs *b* found at the bases of the old tentacles are lacking in the new tentacles at this stage, and form only after the new tentacles have attained considerable growth. This fact has been previously observed and noted by Hargitt[1] 1901. The tentacles

[1] BIOLOGICAL BULLETIN, Vol. II., p. 244.

grew slowly and in two or three weeks some specimens had developed only two to four tentacles, though several small bulbs were present. In other specimens more tentacles formed, Fig. 5

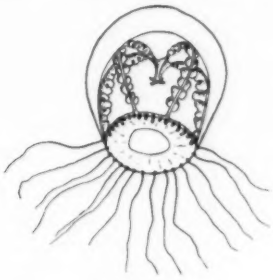

FIG. 5.

showing seventeen bulbs and small tentacles on the regenerated margin.

II. EXPERIMENTS ON THE REGENERATION OF THE MANUBRIUM.

In some cases the manubrium was removed by a circular cut passing entirely through the jelly of the bell. The size of the opening left varied in the different specimens but was not very large in any individual. In other cases the upper half of the bell was removed, thus leaving a very large opening. The rate of healing did not seem to be at all dependent upon the size of the opening, for, as noted below, some of those in which the upper half of the bell was removed took less time to heal than some in which only the manubrium was cut out. In all cases the cut edges gradually contracted till they were touching. As soon as they met they began to fuse and in a very short time the wound was entirely healed. The rate of contraction and healing was not the same in all the specimens.

In the first set the contraction was slow, the cut did not completely heal until 60 hours after the operation. In the second set the contraction was quite rapid. Twelve hours after the operation the cut edges had met and twelve hours later had entirely healed in half the specimens, though in the rest of the specimens of this set 60–70 hours were required. In the third set the cut edges had met and fused at the end of 48 hours. In the

fourth set, although the upper half of the bell was removed, the edges contracted quite rapidly and in 36–48 hours had fused. In this last set the typical bell-shape of the medusa could not be assumed because of the large amount of the bell removed. In contracting the margin was drawn up and when the edges had fused the medusa was flattened and the bell very shallow. Sometimes the center of the bell was depressed (Fig. 6), though this disappeared later. Occasionally the bell was twisted somewhat, the margin turned under and a tentacle thrust through the hole in the top of the bell. This of course delayed the healing of the wound. In the four sets of this experiment, after the cut edges had fused no scar or sign of the fusion was present.

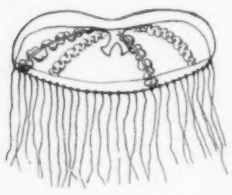

FIG. 6.

By the time the wound in the bell had closed, or very soon after, the free ends of the radial canals had also met and fused. The manubrium developed slowly. In 48–80 hours after the canals had fused a gastric pouch had usually formed. This is simply a large pouch into which the canals lead, and at first has no opening to the exterior. Fig. 7, *a*, shows the gastric pouch before the development of the manubrium. From these pouches the manubria develop. In some cases they had completely formed in four days after the operation. In other cases a week or ten days was necessary for their complete development. Quite common was the formation of double or bifurcated manubria. In the four sets of this experiment 21 per cent. developed double manubria. The formation of the double manubrium was followed out in detail in one specimen. Fig. 7, *a*, shows the large gastric pouch as it first appeared, with no mouth opening. A small diverticulum from this pouch was at first taken for the beginning of a new radial canal, but it developed into another pouch as shown in Fig. 7, *b*. From each of these pouches a

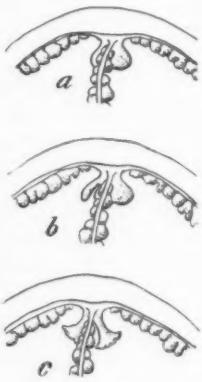

FIG. 7.

manubrium developed as shown in Fig. 7, *c*. All stages were found, from those in which each manubrium was distinct and had a separate pouch, through those in which two manubria were attached to a single pouch, and finally to those in which a single manubrium was branched or bifurcated at its distal end.

The fact that such a considerable per cent. developed double manubria assumes new interest when it is noted that this is not simply the result of artificial mutilation and regeneration. Several specimens of *Gonionema* have been taken from the eel pond near the laboratory, in which double or bifurcated manubria were present. Furthermore, this is not limited to *Gonionema*. During the summer of 1902 a specimen of *Oceania languida* was taken by C. W. Hargitt, in the "tow" in Vineyard Sound, in which two manubria were present. In this specimen three radial canals met normally in the center of the subumbrella. The fourth canal was not complete, extending from the marginal canal only about half way to the center. At the union of the three canals a large four-lobed manubrium was present. At the inner end of the fourth short canal was a small manubrium. This small manubrium was only three-lobed and had three oral frills, and in this resembled some of the regenerated manubria in *Gonionema* which had only two or three lobes. This small manubrium in *Oceania* may perhaps be interpreted as a case of adaptive regeneration. The short canal not having any direct connection with the center of the chymiferous system may have been nearly, if not entirely, deprived of the circulation of the chymiferous fluid, and thus threatened with atrophy; and the new manubrium may have been formed to remedy this condition. This would be more important inasmuch as the gonad on this canal was as perfectly developed as those on the other canals. In both the cases just mentioned both of the manubria were active and functional.

In the second set the wound entirely healed as noted above, and then in two specimens the bell evaginated. The next day the evaginated ones died without having developed manubria or gastric pouches. In one specimen, Fig. 8, the canals did not unite as in former cases but in the form of a ring, and two manubria formed on opposite sides of the ring. They did not form at

the same time, one being formed a day or two earlier than the other. The presence of these rings is not uncommon in specimens otherwise normal, as noted by Hargitt, 1901. As has already been noted, in the fourth set the upper half of the bell was removed. When the wound had healed the bell was flattened and elongated. It was therefore impossible for the canals to unite in the usual way. The two canals at the ends of the elongated bell united and between these two pairs of canals a

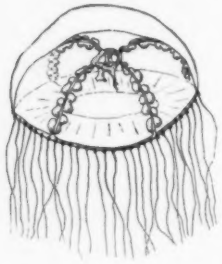

FIG. 8.

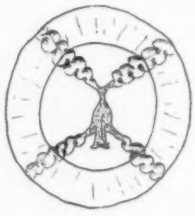

FIG. 9.

straight connecting canal then regenerated, thus completing the chymiferous system. The manubrium then regenerated from these straight connecting canals, but not till the canal was completely formed and functional. If the manubrium formed at the union of the connecting canal with one of the pairs, it was triangular in shape and three-lobed as in Fig. 9. If it formed in the center of the connecting canal it was two- or four-lobed.

III. EXPERIMENTS UPON THE REGENERATION OF THE RADIAL CANALS.

The medusæ were first cut in a vertical interradial plane. Thus each piece had two canals and half the tentacles. The cut sometimes passed through the manubrium and sometimes to one side. Thus some pieces would have a part of the manubrium, others the entire manubrium and in the rest the manubrium would be entirely lacking. The cut edges gradually approached each other and finally met and fused, and the typical medusa-form was thus assumed. Occasionally the manubrium projected between the cut edges and delayed the healing. Usually, how-

ever, the fusion was complete in two to four days. During the process of healing the cut edge of the margin usually drew up somewhat, so that when the fusion was complete there was a scallop or notch in the margin of the bell. The ends of the marginal canal fused and a new radial canal formed along the line of union of the cut edges of the bell. This new canal elongated and the notch in the margin gradually disappeared. Morgan in describing a similar experiment says, "Along the line where the cut edges fused together a scar is present that resembles somewhat a third canal, but the third canal did not develop." While in his experiments this may have been the case, my own show conclusively the development of a third canal. Hargitt, '99, refers to the formation of new canals though he did not demonstrate their functional activity. Along the line of fusion of the cut edges a deposition of pigment is present which might be mistaken for a scar unless carefully examined. At first it is perhaps not a functional canal, but two or three days after the fusion the movement of the chymiferous fluid in the new canal was plainly observed, not only by myself but by others to whom it was pointed out. Furthermore in the closing of the bell, when the oral half had been removed, no sign of a scar or pigmentation was found. Such a scar or pigmented line, therefore, is not simply the sign of the fusion of cut edges, but represent the regeneration of a new organ along what is probably the line of least resistance.

This experiment was varied by cutting out one quadrant with its radial canal, leaving three canals, three quarters of the number of tentacles and the manubrium or a part of the manubrium. The fusion of the cut sides took place in about the same time as in the preceding experiment, though the incidental protrusion of the manubrium through the opening and the consequent delay in healing was more marked. On the fourth day the fusion was complete and a new canal had formed. Fig. 10 shows the new canal at *a*, the scallop in the margin is also shown. The latter gradually disappeared as in the former experiment and the bell margin became quite symmetrical.

The development of gonads on the new canal did not take place while the specimens were under observation. This would undoubtedly occur somewhat slowly if at all. This, however, is

not a constant feature in normal specimens, in many of which gonads are lacking on one or more canals. Occasionally the fusion of the cut edges and the formation of new canals resulted in apparent abnormalities. Fig. 11 shows such a case in which the new canal *a* has anastomosed with one of the old ones. But this again has its counterpart among normal specimens in a state of nature.

The single quadrants which were cut out in the preceding experiment were placed in separate dishes. These contained a single canal, in some cases a part of a manubrium. The contraction of the cut edges took place as usual and in from three to four days the typical medusa-form had been assumed, the edges

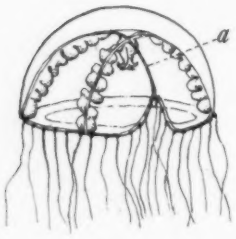

FIG. 10.

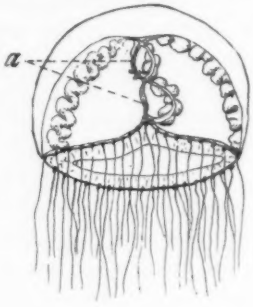

FIG. 11.

of the margin and marginal canal had fused as had also the velum. The apex of the quadrant was flexed toward the margin and when the fusion was complete this portion, and with it the proximal end of the canal, was joined to or very near, the marginal canal. In specimens having a portion of the old manubrium this was also carried downward and fused with the marginal canal and a gastric pouch formed at the point of union, and when the new manubrium was finally regenerated it protruded beyond the edge of the velum in the same horizontal plane. In specimens where no portion of the old manubrium was present usually entirely new ones regenerated but in the same general position as in the former. These new medusæ were of course only about one fourth the size of the original specimen and with only a proportional number of tentacles.

Summary and Review.

Hargitt, '97, showed for the first time that a medusa when divided into two or several pieces had the capacity to recover the original form, and that various organs, as manubria, canals and tentacles, were also regenerated. He also showed that the process was a gradual and orderly one. Further experiments in '99 by the same author showed that at least in case of radial canals and manubria the process was one of actual generation of new tissue and not merely the recasting of parts of old tissue into new forms.

Morgan, '99, experimenting on the same medusæ, confirmed these results to a certain extent, but claimed that new canals were not regenerated. He showed, moreover, that when cut into quadrants or smaller portions while a similar recovery of form was common, the resulting medusa was not typical in that in many cases there were lacking certains organs, as the typical number of canals, gonads, etc. And furthermore in case of smaller pieces where new manubria were regenerated it was not in the normal position. This observer also claimed that where only a portion of the margin was removed the regeneration of tentacles was more prompt and better developed than where the emargination had been complete.

As will have been seen, my own experiments confirm in part those of both these observers, and in part extend their results, by showing conclusively the regeneration and *functional activity* of both radial and marginal canals. My experiments show that when the division of the medusa was in vertical interradial planes that the resulting half medusæ were almost always perfectly symmetrical, while Morgan claimed they were otherwise, in that the manubrium was eccentrically located. This, so far as my experiments go, was only true when the section itself was quite unequal.

I was also able to obtain better results in regeneration of tentacles than either of the authors named, as an inspection of several of the figures will show. Concerning the experiments upon small pieces of medusæ, and regeneration of tentacles of partially emarginated specimens my own confirmed in almost all details those of Morgan.

As to the *processes* involved in these phases of regeneration my experiments confirm in the main those of both Hargitt and Morgan.

Hargitt, '97, says concerning it, "there seems to be an intrinsic potency to recast itself into the morphological equivalent of the original." Morgan says the process "is one of rounding up of the piece in direction of least resistance. The meeting of the edges may sometimes be due to simple accidental meeting of the bent-in portions." My own experiments showed no evidence of a merely accidental or mechanical process, but rather self-directive activity inherent in each portion of the individual. The process was in all cases gradual and orderly and the meeting of the edges too exact and certain to be explained as the result of mere accident.

SYRACUSE UNIVERSITY, THE ZOÖLOGICAL LABORATORY,
September 10, 1902.

NOTES ON A FEW MEDUSÆ NEW TO WOODS HOLL.

CHAS. W. HARGITT.

The following notes on a few medusæ taken during the current summer in the region of Woods Holl may serve as a preliminary account of work under way which will present a synopsis of the medusoid fauna of the region and which it is hoped may be ready within the year.

During the summer several expeditions for collecting were made to localities within fifty to seventy-five miles, most of which were made within a single day on board the launch "Phalarope," of the United States Fish Commission Laboratory, under direction of Dr. H. M. Smith, to whose courtesy I am under obligations, as also to Mr. Vinal N. Edwards for many favors.

The first excursion, and the one most prolific in specimens, was made to the region of the Gulf Stream, known as the Tile-fishing Station, latitude 40° 10′ 45″, longitute 70° 20′ 30″, by the schooner "Grampus," Captain Hahn, July 30 to August 2.

The material was taken by means of the tow-net, mostly from the surface, though in a few cases hauls were made from depths of from fifteen to twenty-five fathoms. Further reference to results of these deeper hauls will be made in another connection.

The medusæ taken include representatives of at least twelve genera and probably eighteen species. Several species of siphonophores are as yet undetermined. Specimens of *Oceania languida* and of *Epenthesis foliata* were very abundant, but these were taken most plentifully near Gay Head and No Mans Land. The following named species have been identified and of those not formerly recorded sketches and brief descriptions are given.

Oceania languida, taken in great abundance chiefly from a depth of about fifteen fathoms in water of seventeen fathoms. They were taken in the surface tow but in fewer numbers.

Epenthesis foliata, likewise taken in considerable numbers at similar ranges of depth.

Very few specimens of *Bougainvilla superciliaris* partly from the surface and partly from a lower depth.

Nemopsis bachei, about twenty specimens taken from deeper towing in Vineyard Sound.

Lafœa calcarata taken in surface tow near Gulf Stream. This is more usually a littoral form and its presence at this distance from land is not common. It is fairly common in the surface tow at Woods Holl.

Obelia were found in considerable numbers at the surface and near shore. Several species were taken, two of which, *O. geniculata* and *O. flabellata* were most common.

Aglaura hemistoma, numerous specimens taken at surface near the Gulf Stream. So far as I am aware this is the first record of this medusa within this region. The following cut, Fig. 1,

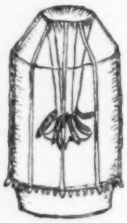

FIG. 1.

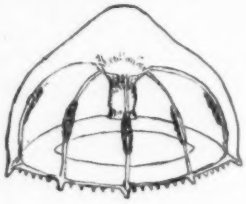

FIG. 2.

will give a good general impression of this beautiful medusa. In size the specimens varied from two to four mm. in height by about half that in width. It was not possible to distinguish any sense organs on the specimens, the preservation in formalin having apparently rendered the otocysts, if present, indistinguishable. Incidentally it may be mentioned that this is a familiar effect with specimens preserved in formalin of any considerable strength. Even in 5 per cent. solutions it has this effect in many cases. The oral end of the manubrium is reddish in color, the gonads, which are borne just above the gastric pouch, are yellowish-white or brownish. The peduncle of the manubrium is long and gelatinous. In the specimens the tentacles had all been apparently broken off close to the margin so that only the short bases were remaining. Radial canals are eight in number and extend downward upon the peduncle.

Several specimens of an interesting Trachynemid were taken in the same locality. Most of them were considerably damaged,

and like the specimens of *Aglaura* were devoid of tentacles. Fig. 2 will give a good impression of the medusa. In size the specimens varied from 6 to 10 mm. in broad diameter by slightly more than half as high. Bell subhemispherical in shape with a solid apical projection. Radial canals eight in number, and with gonads borne about the median region on the under side. Manubrium urn-shaped and with flaring, slightly quadrate lips. Color transparent, with an evident iridescence, manubrium dull white, as are also the gonads in formalin specimens. In most respects it agrees fairly well with the description of *Rhopalonema typicum* Maas. from the west coast of Mexico, and later by Agassiz and Mayer from the tropical Pacific.[1]

While the occurrence of the same species in a comparatively

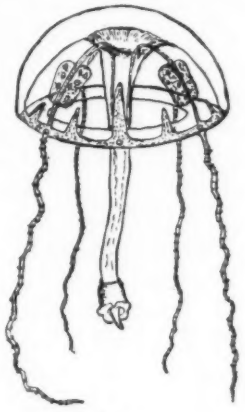

FIG. 3.

high latitude of the Atlantic might seem somewhat improbable, still I am not able to distinguish sufficient differences in specific characters to warrant considering it a new species. As intimated above, the somewhat damaged condition of the specimens and inability to distinguish otocysts may afford characters when determined to justify a different conclusion.

In Fig. 3 is shown another medusa not hitherto recorded from the region. As will be seen it bears some resemblance to the

[1] Cf. Mem. Mus. Comp. Zoöl., Vol. XXVI., No. 3.

Liriope scutigera McCr., but closer inspection will show that in several respects it differs very materially. It would seem to be much closer related to *L. cerassiformis.* Specimens of various sizes showed the various phases in the development and atrophy of the secondary, interradial tentacles, so that in the adult there are only the four perradial tentacles. They were taken in the surface tow near the Gulf Stream. In size the adult specimens were about 10 mm. broad by slightly more than half this height. Bell very transparent, gonads opaque, somewhat shield-shaded, and showing ova in various stages of growth. The centripetal canals were twelve in number, the interradial set being about twice the size of the adradial set. It should be noted that these were exceedingly difficult to distinguish on superficial examination, and this may in part account for their apparent absence in the earlier figures of *L. scutigera.*

In Fig. 4 is shown another medusa taken near No Mans Land

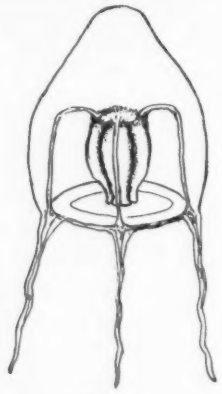

FIG. 4.

on two different occasions during the summer and apparently entirely new to science. Several specimens were taken in the same general locality between that above mentioned and the Gulf Stream. In shape the bell is somewhat oblong, with an extended apical projection. Gastric portion of the manubrium rather large and subquadrate in cross section, mouth simple and with slightly everted lobes; gonads in four rather prominent masses surround-

ing the manubrium. Tentacles four, with rather prominent basal bulbs, hollow, attenuate in shape and densely crowded with nematocysts. Velum well developed; ocelli absent; height of bell 2–4 mm. by about half as broad. Color, bell transparent, gonads and manubrium milky white.

While the medusa has characters which indicate relations with the Codonidæ, *e. g.*, the simple mouth opening, straight, simple tentacles, general shape, etc., it has likewise characters which also point to relations with the Tiaridæ, such as the subquadratic manubrium, lobular arrangement of gonads on the radial sides of the manubrium, and the apical projection of the bell. From a critical comparison of the sum of the characters with Hæckel's description of the genus *Protiara* which he established for a medusa which in general characters appears to have much in common with the one under consideration, it seems to find its place appropriately under this generic head, and may be taken to constitute a sort of connecting link between the two families, since Hæckel designates his as the prototype of the Tiaridæ, and most nearly allied to the Sarsiadæ of any of the Tiarids.

But while undoubtedly allied with *Protiara* it is clearly a distinct species, differing in almost all its specific characters, as color, shape, etc. For the present species I propose the name *P. hæckeli*, in honor of the author of the genus under which it falls.

As intimated above several species of Siphonphores were taken in this collection which have not been determined and since they are not at present accessible further account of them will be deferred till such time as they may have adequate description.

In Fig. 5 is shown an interesting Narcomedusa taken also in surface tow near the Gulf Stream. Only a single specimen was taken and this was slightly damaged and apparently immature, having only four perradial tentacles with what seem to be very small interradial tentacles. As in several of the previously mentioned cases, it was not possible to distinguish any sensory bodies. The specimen is a member of the Solmaridæ, and perhaps belongs to the genus *Solmaris*, but in view of its apparent immaturity, indicated by the absence of gonads and undeveloped interradial tentacles, it seems probable that it may be the young

of some *Solmaris*. It is perfectly evident that in its present stage of development it does not find close relations with any species at present distinguished. Should further collections of other similar specimens of similar characters justify specific distinctness I would propose for the species the name of *S. tetranema*.

A somewhat rare Scyphomedusa for this region was taken near

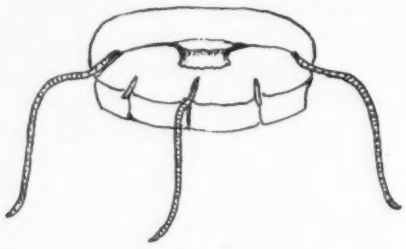

FIG. 5.

the Gulf Stream in the locality indicated in the introductory paragraph, namely, *Pelagia cyanella*. So far as I know the only previous record was of a single specimen taken by the "Fish Hawk" in 1899 in essentially the same region.

The specimen measured about 30 mm. in diameter, being immature, as no marked development of gonads had yet occurred. The previous specimen measured about 50 mm. in diameter and was loaded with well-developed ova apparently ready to be discharged. This is one of the few distinctly pelagic medusæ of this class which occasionally come within the limits of the region, and is at the same time one of the most beautiful, rivalling *Dactylometra*, if not surpassing it in the richness and delicacy of its coloring and grace of form. A fuller description of the medusa will be given in a later contribution.

In this connection may be described an interesting medusa taken in the tow in Great Harbor, Woods Holl, on the evening of August 16. Its general form is well illustrated in Fig. 6. The following brief characters may further differentiate it: Bell subrectangular in profile with a slight apical projection, bell walls rather thin and very transparent, capable of great contraction in both directions; radial canals four, rather wide and simple; manubrium sessile, with broad base and tapering to a terminal

oral orifice which is simple and slightly four lobed. Tentacles four, unequally developed, probably due to immaturity. The two on opposite sides (right and left of the figure) presenting the relative size and form, which are quite unique among medusæ of this family (the Codonidæ), though somewhat like greatly exaggerated tentacles of *Dipurena*. In addition to the enlarged terminal knobs which are densely packed with nematocysts, each teniacle has a distinct ring of nematocysts about the middle of the stalk as shown in the figure. In size the medusa measured in life about 2 mm. in height by about 1.5 mm. in breadth. The

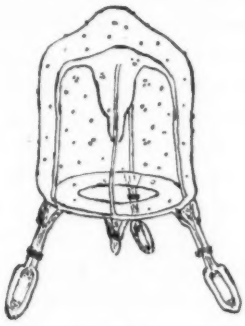

FIG. 6.

exumbrellar surface was irregularly and sparingly dotted with minute clusters of nematocysts. In color the specimen was brilliantly marked, the terminal bulbs of the tentacles being at the apex brilliant carmine tinged with green, and their basal portion duller reddish-brown; the basal bulbs similarly reddish-brown with a dense black ocellus on the outer side. The manubrium was tinged with pale green. It should have been said that the two undeveloped tentacles were not equally so, one being in all but size quite like the larger pair while the smaller one, though much smaller than the other, was evidently lacking in age only to attain to the size and form of the others.

The specimen (only a single one being taken) bears indications of immaturity; *e. g.*, the unequally developed tentacles, absence of distinct gonads, and the nematocysts of the exumbrellar surface. In view of the similarity of swimming habit, coloration,

and the general aspect of tentacles, the first thought was of its possibility as the very young of *Dipurena*. A careful study of the bell form, as well as that of the manubrium, and the remarkable development of the tentacular knobs, all are fundamentally unlike *Dipurena*. And while apparently a young specimen it may be doubted whether in all essential respects it is not fairly adult in morphological aspects. I am therefore disposed to regard it as entitled to both generic and specific distinctness, and propose for it, at least provisionally, the name *Dipurella clavata*.

Cruises were made off Nantucket southward on August 13, and off Chatham at "crab ledge" August 19 secured a medusoid fauna in many regards different from that of the former. *Oceania* and *Obelia* were found in about the same numbers as before, but there was a noticeable absence of all those distinctively tropical in their ranges.

On the other hand here were the outliers of an arctic fauna as indicated in such forms as *Pleurobrachia* and *Beroe* among Ctenophores, *Tealia crassicornis*, *Bunodes stella*, among actinians, *Solaster* among starfishes, etc., while of medusæ were found *Hybocodon*, *Corymorpha* and *Trachynema* chiefly.

The occurrence of *Hybocodon prolifer* at this season was quite a surprise, as so far as I am aware its occurrence has been recorded chiefly, if not wholly, during the very early spring. It was in perfect sexual maturity and also budding medusæ proliferously from the base of the tentacle. An interesting condition of these specimens was the absence of the bright orange-red coloration which is so marked a feature of the early spring forms, and with it also the absence of the exumbrellar bands of nematocysts. But for the fact that I have often noted the gradual decline of this feature in late spring specimens I should have felt disposed to consider the specimens taken on this cruise to be of a distinct species. It is not altogether improbable that similar features in the seasonal variation of other medusæ may have been the occasion of thus specifically differentiating one and the same organism.

Here also I took for the first time during the summer the medusa of *Corymorpha pendula*. In general aspects it is much like *Hybocodon* and I am disposed to favor Haeckel's assignment

of this medusa to the latter genus. While less marked by asymmetry than is *Hybocodon*, and while having only one perfectly rudimentary tentacle, these do not seem sufficient grounds upon which to establish a distinct genus.

Another interesting medusæ taken at both these stations and apparently a new species, is closely related to *Trachynema digitale*, and was at first considered to be the young of this species. A closer examination, however, showed it to be quite specifically distinct. Fig. 7 will afford a good general impression of the morphological aspects of the medusa. In size it averages about five to six mm. in height, by three mm. in width of bell. This of itself might not justify the conclusion of specific distinction, still as an average of about fifty specimens, taken at considerable distances and at an interval of nearly a fortnight, it would strongly warrant such a probability, when we know the

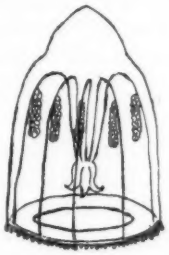

FIG. 7.

former species to have an average of from twenty-five to thirty-five mm. in bell height by about half that width.

Again the color of the former species is quite strongly in contrast with that of the medusa under consideration. In *T. digitale* the bell is said to be light pink, the manubrium reddish and the tentacles at the contracted tips also red. The present species is wholly devoid of color, except for the slightest tint of pinkish iridescence which at times appears under favorable circumstances.

Haeckel has placed Agassiz' species under a different family, the Aglauridæ, and under the new genus *Aglantha*. This readjustment is apparently well founded, and I, therefore, incline to

accept it and to propose for the species under consideration the name *Aglantha conica* the specific name designating the somewhat typical cone shape of the medusa.

The following specific diagnosis briefly summarizes the more distinctive characters of the medusa: Bell high with rather sharp apical projection slightly constricted just above the bell cavity. Manubrium long and with elongate gelatinous peduncle; gastric region only about one fourth as long as the former and with prominent four-lobed lips, the whole organ about three fourths as long as the bell cavity. Radial canals eight, extending the length of the peduncle. Gonads eight, cylindrical and suspended from the upper portion of the bell cavity under the canals. Velum well developed and apparently strongly functional as the organ of locomotion; movements of the medusa active and erratic, darting arrow-like when disturbed; bell walls thin with tendency to wrinkle longitudinally when placed in formalin. Tentacles apparently numerous, though mostly lacking, only the bases generally distinguishable; those present were short and rather blunt. No marginal organs or otocysts distinguishable.

The specimens were taken with the open tow-net at a depth of from twelve to sixteen fathoms. Many of the specimens were sexually mature, some females discharging eggs. Both sexes apparently present and in about equal numbers.

These observations would seem in the main to confirm the earlier records of Stimpson, Agassiz, Verrill, Packard and others that the point of Cape Cod marks a limit more or less definite, between a boreal, or "Acadian," and a "Virginian" fauna which pertains to not only cœlenterate life but to a considerable range of invertebrates. Undoubtedly the configuration of the coast line and its associated topography in their influence on the various currents are important factors in the faunal ranges which are under consideration.

In this connection may be discussed another point to which previous reference has been made, namely, the varying depths from which our hauls were made. I regret to say that the nets were only of the ordinary open sort, which therefore precludes anything like exact data, but the repetition of hauls at the same

place and from varying depths and a careful comparison of results afford a rough approximation toward an estimate of the relative abundance of life at given depths as compared with the surface, as well as the varying kind of life at the several depths.

In the more open ocean and in the region of the Gulf Stream the larger number and variety were obtained almost entirely from the surface. In the regions of No Mans Land, Nantucket, Chatham Ledge, Vineyard Sound and Buzzard's Bay, on the other hand, a greater abundance and variety of medusæ were obtained from a depth of from 10 to 15 fathoms in water of 17 to 25 fathoms than from either the surface or the bottom. This was more particularly true in rough water and during midday or in bright sunshine. Surface towing during late evening or on dark days most generally give a much larger average in the abundance and variety of species.

In a general way these results, which I have often observed also in previous years, confirm the observations of others and tend to establish what may be considered a law of pelagic life in its relations to light and other aspects of surface environment. At the same time it should not be overlooked, that occasionally there seem to be marked exceptions to such a law. I have taken at times these same forms from the surface in almost incredible abundance, so abundant indeed that with an ordinary pail one might take hundreds at a single dip. Whether sexual conditions, as Agassiz has suggested, or some other condition at present imperfectly known or understood may not be involved it may remain for the future to determine. That sexual conditions *alone* are determining factors seem to me more than doubtful. I should rather incline to consider temperature or tidal currents as probably important factors in the case, just as it seems to me that prevailing winds and currents account for the presence of large numbers of *Aurelia*, *Cyanea*, or other of the Scyphomedusæ, in bays or protected harbors rather than that such segregations are for breeding purposes.

SYRACUSE UNIVERSITY, THE ZOÖLOGICAL LABORATORY,
September 2, 1902.

ON THE MORPHOLOGY OF THE CHROMOSOME GROUP IN BRACHYSTOLA MAGNA.

WALTER S. SUTTON.

The appearance of Boveri's recent remarkable paper[1] on the analysis of the nucleus by means of observations on double-fertilized eggs has prompted me to make a preliminary communication of certain results obtained in a general study of the germ-cells of the great "lubber grasshopper," *Brachystola magna*.

As will appear from a glance at the figures given in my former paper[2] upon the same form, the cells of *Brachystola*, like those of many amphibia, selachians and insects and certain of the flowering plants, exhibit a chromosome group, the members of which show distinct differences in size. Accordingly, one feature of this later study has been a critical examination of large numbers of dividing cells (mainly from the testis) in order to determine whether, as has usually been taken for granted, these differences are merely a matter of chance, or whether, in accordance with the view recently expressed by Montgomery,[3] in regard to a certain pair of elements in the nuclei of one of the Hemiptera, characteristic size-relations are a constant attribute of the chromosomes individually considered. With the aid of camera drawings of the chromosome group in the various cell-generations, I will give below a brief account of the evidence which has led me to adopt the latter conclusion.

In the first generation of secondary spermatogonia, which are the earliest germ-cells I have been able to obtain in *Brachystola*, certain differences in length and volume are to be seen between the members of the chromosome group. These cells, as shown in my former paper already referred to (where they are errone-

[1] Boveri, Th. (1902), "Mehrpolige Mitosen als Mittel zur Analyse des Zellkerns," *Verh. d. Phys. Med. Ges. zu Würzburg*, XXXV.

[2] Sutton, W. S. (1900), "The Spermatogonial Divisions in *Brachystola magna*," *Kans. Univ. Quart.*, Vol. 9.

[3] Montgomery, T. H., Jr. (1901), "A Study of the Chromosomes of the Germ Cells of the Metazoa," *Trans. Amer. Phil. Soc.*, Vol. XX.

ously described as the last generation of primary spermatogonia), lie in the follicle without definite arrangement and are usually much flattened and distorted by mutual pressure and that of the growing spermatocysts between which they lie. For this reason a study of the chromosome series is difficult in this cell-generation, but, fortunately, I have been able to find a few division-figures which permit of an accurate study of the chromosomes. Such a cell as that shown in Fig. 1—a metaphase in polar view—offers the best opportunities. Here it is apparent at a glance that the chromosomes are of a variety of sizes, but yet in general so nicely graded as to form an almost regular series from smallest to largest. A second glance, however, reveals the fact that there is one very prominent break in this graded series, separating the six smaller chromosomes from the remaining larger ones, and a count of the larger group shows it to contain seventeen units, giving as a total the odd number twenty-three.[1] The odd or twenty-third member of the group, as can be plainly seen in the following division, is the accessory chromosome, which on account of its peculiar behavior will be considered separately. There is, therefore, in the ordinary group, the even number, twenty-two. More especially in the smaller group, but likewise in the members of the sixteen, it can be seen that the gradations in volume are not between individual chomosomes but between pairs, the two members of which in each case are of approximately equal

FIG. 1.

FIG. 1. Polar view of metaphase of first generation of secondary spermatogonia. Six small chromosomes designated by letters *i*, *j* and *k*. (From section.) *Note.*—All figures given in this paper are camera lucida copies of the portions under consideration from the original camera drawings to be published in the forthcoming work to which this is preliminary. The figures are not schematized.

[1] Montgomery (*l. c.*) has found four of the Hemiptera-heteroptera to possess an odd somatic number of chromosomes and I have observed the same to be true for some fifty species of Acrididæ and Tryxalinæ.

size. In other words, there are, in the ordinary chromosome group, not twenty-two but eleven sizes of chromosomes. The lettering in the figure will indicate the pairs in the smaller group where they are most clearly defined.

Eight[1] generations of spermatogonia follow this one, and in each succeeding metaphase the same number and size-relations of chromosomes may be observed. This is shown in Figs. 2 and 3, representing different secondary spermatogonial generations,

FIG. 2. FIG 3.

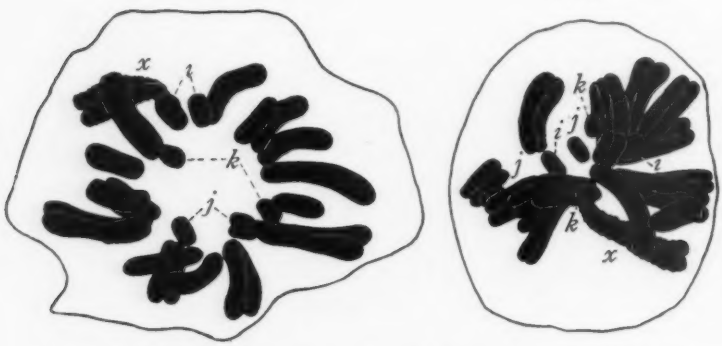

FIG. 2. Polar view of equatorial plate in secondary spermatogonium of one of the earlier generations. (From section.)

FIG. 3. Oblique lateral view of equatorial plate of a secondary spermatogonium of one of the later generations. (From a smear-preparation.) Small chromosomes and accessory designated as in Fig. 1.

in each of which appears six small chromosomes and seventeen larger ones. In each of these also — especially in the case of the smaller group, the members of which, on account of their nearly spherical form, do not suffer the same degree of foreshortening in the drawing as do many of their longer comrades — the paired relation may again be made out. Moreover, in the smaller group with its fewer members and greater size-differences, it is possible to see that the volume of the smallest pair (*kk*), for instance, in one cell bears approximately the same ratio to the homologous pair in another cell as does that of the largest (*jj*) of the

[1] Based on estimates of the number of cells in a spermatocyst at the time of transformation to spermatocytes.

first cell to the largest of the second, or the middle-sized pair (*ii*) of the one to the middle-sized pair of the other. In these cells the compact condition of the chromosomes will not permit of the accurate recognition of individual elements — other than perhaps the largest and the smallest — in the group of sixteen, where size differences are comparatively slight, but this deficiency will be made up in the consideration of the group in the spermatocytes.

Throughout all the secondary spermatogonial generations, in all stages except those of active division, the accessory chromosome remains apart in a vesicle which is virtually a separate nucleus. The genetic relation of the accessory chromosome of any secondary spermatogonium to that of any other in its line of ancestry seems, therefore, unquestionable. Each of the sixteen chromosomes of the larger group has also been enclosed in a separate vesicle (Fig. 4) during the period of metabolic activity,

FIG. 4.

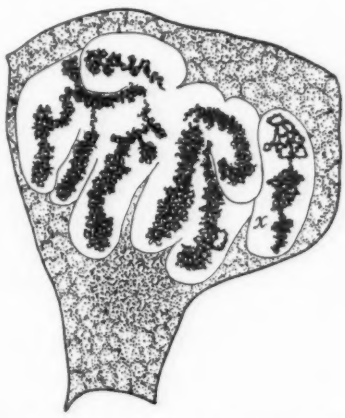

FIG. 4. Secondary spermatogonium in early prophase, showing very fine spiremes arranged in their respective diverticula of the nucleus. Most of the partition walls between diverticula are shorter in the figures than in the preparation, since their crossing if drawn in full would only cause confusion in a line drawing. (From a section.)

but these vesicles are practically always in communication with one another at their polar extremities, forming there a common compartment in which the six smaller units are frequently found.

In this case there is plainly a possibility for an exchange of chromatic matter; but since each generation exhibits the same series of chromosomes as that before; and since, after the stages of the very fine spireme, the chromosomes reappear one in each sacculation as before, no other conclusion seems credible than that they are, chromosome for chromosome, the same in one generation as in another, just as is the case with the accessory.

During the transformation to spermatocytes, the nucleus as a whole becomes spherical, but, in many cases, the compartments still remain; and in them the chromosomes pass through the fine spireme stages. In this condition, as in that just described for the spermatogonia, it is difficult to conceive the formation of a continuous spireme; but when, at a little later stage, cell and nuclear membranes have become less resistant so that their contents may be smeared upon cover-glasses and there fixed for study *in toto*, it becomes clear that fewer spiremes are present than in the spermatogonial nuclei. In every case, the accessory chromosome appears in its peculiar characteristic condition (*x*, Figs. 5 *a*, 5 *b*, 6 and 7), and careful counting of a large number of cases *shows the spiremes in every favorable instance to number eleven.* These spiremes are graded as to size just as were the chromosome-pairs of the spermatogonia; and the gap in the series separates a group of *eight large* from a group of *three small* elements. In most of the spiremes a longitudinal split is clearly visible, and in addition, in practically every case, a division may be noted separating the spireme into two distinct limbs of approximately equal size, which are frequently doubled on each other at the point of union.

If now we seek the relation of these spiremes to the chromosomes of the spermatogonia, we find abundant data. Twenty-two chromosomes enclosed in separate compartments, each opening at one end into a common chamber, are represented by eleven double chromosomes. Scarcely any two of the eleven are even approximately of the same size, whereas each of the twenty-two appeared to have a mate of like volume. But the eleven double chromosomes are made up each of two limbs of equal size and we find it difficult to believe that these limbs do not represent the members of the pairs, joined together at their polar ends,

FIG. 5a. FIG. 5b.

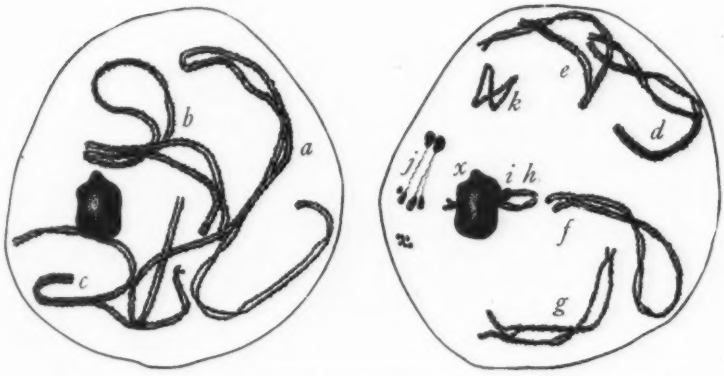

FIG. 5a. Three largest spiremes and accessory chromosome from a primary spermatocyte in early prophase. (Smear-preparation.)

FIG. 5b. Eight remaining chromosomes and accessory from same cell as Fig. 5a.

FIG. 6. FIG. 7.

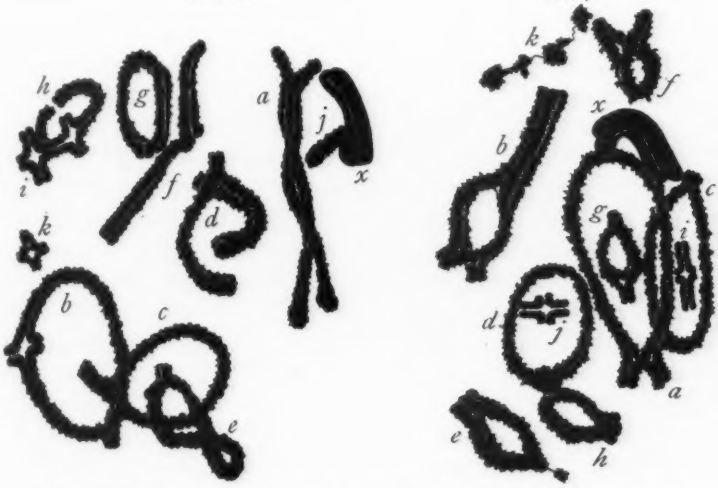

FIG. 6. Partly condensed spiremes in middle prophase of primary spermatocyte. All the chromosomes, including the accessory (x), show indications of a longitudinal split.

FIG. 7. Slightly more advanced chromosome group than that of Fig. 6. Letters a, b, c, d, e, f, g, h, i, j and k designate the different chromosomes in order of size from largest to smallest; x designates the accessory.

which, as we have seen, projected into a common chamber of the nucleus. To such a conclusion additional weight is added by the occasional finding of telophases of the last spermatogonial generation which actually shows such a fusion (Fig. 8).

FIG. 8.

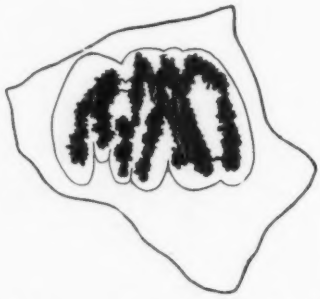

FIG. 8. Telophase of secondary spermatogonium of the last generation showing synapsis. Only a few of the chromosomes are shown and as in Fig. 4; to avoid confusion the sacculations are drawn only to the point where they cross one another.

The four parts of each spireme, marked off by the longitudinal split and the line of fusion, may be traced through all the prophases up to the metaphase, where they are clearly seen to become the four parts of the tetrad. These facts seem to me to leave no escape from the conclusion that in the completed tetrad the longitudinal split represents merely the usual division of a chromosome into equivalent chromatids; but *the transverse marking separates two spermatogonial chromosomes which have conjugated end-to-end in synapsis.*[1]

Notwithstanding the fact that no continuous spireme is formed, the various spiremes of the larger group (16 in spermatogonia, 8 in spermatocytes) in any nucleus are at any given period always of approximately the same diameter and the same degree of concentration. Their respective lengths may therefore be taken as a measure of their respective volumes, and accordingly the longer

[1] Cf. Montgomery, T. H., Jr. (1901), "The Spermatogenesis of *Peripatus* (*Peripatopsis*) *Balfouri* up to the Formation of the Spermatid," *Zool. Jahrb.*, XV.; also "A Study of the Chromosomes of the Germ Cells of the Metazoa," *Trans. Amer. Phil. Soc.*, Vol. XX.

and more slender the spiremes, the more pronounced their differences of volume would appear. Obviously, it is impossible to study the length of convoluted spiremes in sections. Smear-preparations also fail in the spermatogonia on account of the strength of the nuclear membrane, which in these cells resists the roughest treatment and prevents the separation of its contained spiremes. But in the prophases of the primary spermatocytes the nuclear membrane becomes so thin and weak that its contents may be readily smeared upon a cover-glass and the spiremes thus separated and to a certain extent flattened in the plane of the cover. In the most favorable of these cases, such as those shown in Figs. 5, 6 and 7, which represent different stages in the concentration of the spermatocyte spiremes, a more or less accurate comparison by means of measurements is possible. For the sake of convenience in reference, we will designate the chromosomes in these figures by the first eleven letters of the alphabet, beginning with the longest chromosome and proceeding according to size. The chromosomes as drawn are in all cases simple projections and hence suffer a greater or less amount of foreshortening according to the degree of their curvature or inclination to the plane of the slide. This, however, is so slight that it has been disregarded in the table except in case of chromosomes *b* and *h* of Fig. 6. In these cases, the actual length in the figure is given in parentheses and an estimate of the real length in the regular column. No attempt was made to measure the three smaller elements, as their variations in form and diameter in the spermatocytes render measurement in one

	Fig. 5.	Fig. 6.	Fig. 7.
a	43	22	21
b	$32\frac{1}{2}$	$19\frac{1}{2}$ (17)	17
c	23	$15\frac{1}{2}$	15
d	20	14	12
e	$17\frac{1}{2}$	$12\frac{1}{2}$	9
f	$16\frac{1}{2}$	$10\frac{2}{3}$	$7\frac{2}{3}$
g	15	9	$7\frac{1}{2}$
h	$(7\frac{1}{2})$	$8\frac{1}{2}(7\frac{2}{3})$	7
i			
j			
k			

NOTE. — The figures are in terms of an arbitrary unit equivalent to the distance apart of the divider-points used in making the measurements.

dimension of no value whatever. Naturally these figures can make no pretensions to complete accuracy but as approximations they serve to show a uniformity in the different nuclei that cannot justly be ascribed to chance. It is worthy of note that the only case in which a chromosome does not bear approximately the same ratio as its mates to the homologous members of the other two series is chromosome *h* of Fig. 5; which being hidden for the most part behind the accessory, is at best a doubtful quantity.

When the ordinary chromosomes divide in the first mitosis of the spermatocytes, the separation takes place along the line of the longitudinal split and therefore, except that the chromosomes are joined together by pairs, differs in no respect from an ordinary spermatogonial division. The accessory chromosome, however, though showing a clearly-defined longitudinal split, *does not divide but passes entire to one pole*, as Sinéty[1] has independently observed in the Phasmidæ; and after completion of the division may be clearly seen in one only of the two daughter cells, where it is sharply contrasted with the partially disintegrated ordinary chromosomes.

FIG. 9.

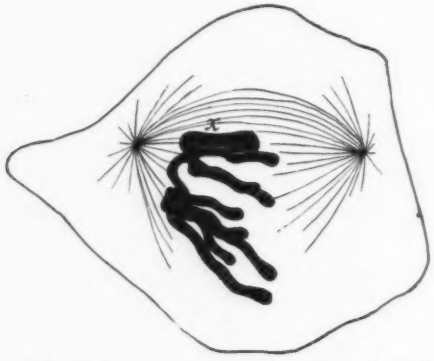

Fig. 9. Four ordinary chromosomes and accessory from a very late prophase of the secondary spermatocyte division. Each ordinary chromosome is made up of two limbs connected at one end. There is no longitudinal split.

In the prophases of the second division the chromosomes reappear in the same number and show the same size relation as in

[1] Sinéty, R. de (1901), "Recherches sur la biologie et l'Anatomie des Phasmes," *La Cellule*, T. XIX.

the preceding telophase, but instead of exhibiting a longitudinal split *they are seen to be composed of two equal limbs joined together at one end only* (Fig. 9) *just as when they passed to the pole in the previous anaphases.* The division occurs at the point of junction of the two limbs and is unquestionably transverse — *separating the two chromosomes at the point where they fused in synapsis two generations before.*

In those secondary spermatocytes in which the accessory chromosome occurs, this element also divides, but in the line of the longitudinal split which has persisted from the prophases of the primary generation. One half of the resulting spermatids, therefore, are characterized by the presence of the accessory and the other half by its absence, but this constitutes the only morphological difference between the two categories. In each, the ordinary chromosomes may be seen to constitute a graded series of eleven members in which a considerable gap at one point separates a subgroup of three small units from another sub-

FIG. 10. FIG. 11.

FIG. 10. Polar view of chromosome group in metaphase of secondary spermatocyte containing the accessory chromosome. Eight large and three small ordinary chromosomes appear. (From section.)

FIG. 11. Axial view of chromosome group of ovarian follicle-cell in telophase. Twenty-two chromosomes appear of which six are decidedly small and the other sixteen decidedly larger.

group of eight larger ones (Fig. 10). The series therefore represent exactly half of the ordinary chromosome group as we found it throughout the secondary spermatogonia. This is the chro-

mosome series which forms the chromatic portion of the sperm-head and consequently is to be regarded *a priori* as the series which will reappear in the sperm-nucleus in the act of fertilization. If this is true — and everything speaks for and nothing definitely against the correctness of the assumption — then the conclusion seems unavoidable that the mate to each of the eleven chromosomes must be furnished by the egg-nucleus to produce the eleven pairs characteristic of all the early germ-cells, of the follicle-cells of the ovary as shown by Fig. 11, and probably also of the ordinary somatic cells.[1]

To sum up, in *Brachystola* the nuclei, not only of the pre-synaptic germ-cells, but also of cells which have been shunted off from the germinal cycle, are characterized by the possession of a chromosome group made up of two morphologically equivalent series of eleven members each.[2] Comparison shows that the size-relations between various members of these series are approximately the same in different nuclei of the same or different cell generations. The numerical reduction (pseudo-reduction) is accomplished by the union of homologous members of the two series of a nucleus, and this union is terminated in the second spermatocyte division by the separation of the daughter-chromosomes of the original conjoints at their point of union and their passage to opposite poles. We are virtually able to recognize each chromosome in eleven consecutive cell-generations; and in the prophases and telophases of nine of these, the chromosomes are separated from one another for a great part of their length, only their polar ends lying in the common chamber. No continuous spireme is formed; and although after each division there is a brief interval, during which chromosomic boundaries can no longer be traced, the regular correspondence, unit for unit, of the mother series with the daughter series establishes a high probability that we are dealing with morphologically distinct individuals, each of which bears to its mother element a genetic relation

[1] Cases of cells other than germ-cells in which an accurate count of the chromosomes is possible are extremely rare on account of the crowded condition of their nuclei; but I am able to state that in the cells of the ovarian follicles and of the common collecting ducts of the testes every division figure shows large and small chromosomes in apparently the same relation as those found in the spermatogonia.

[2] Besides the accessory chromosome.

comparable to that existing between mother- and daughter-cells.

I have endeavored to show that the eleven ordinary chromosomes which enter the nucleus of each spermatid are selected one from each of the eleven pairs which made up the double series of the spermatogonia. It now becomes a highly interesting question whether there exists in the ripe egg a graded series of chromosomes similar to that of the mature male element. I have found the chromosome group not only of the oögonia but also of the ovarian follicle cells (Fig. 11) to correspond perfectly with that of the spermatogonia; and if we are permitted to assume that the reduction process in both sexes is the same, we have no alternative but to believe that the chromosome series of the mature germinal products also are alike. Obviously, copulation of such nuclei in fertilization would restore the conditions which we have found not only in the early germ-cells but in some outside the line of succession.

These latter observations have totally disregarded the accessory chromosome, but it is in it, if further research shall substantiate my present limited but thoroughly consistent results, that we shall find our most unequivocal evidence of chromosomic individuality. We have noted that the spermatogonia have twenty-three chromosomes, and that the odd one of these is the accessory which by means of its idiosyncrasies may readily be recognized in all except the active mitotic stages. We have also noticed that this element is unequally distributed in the maturation divisions and as a consequence occurs in exactly half the spermatozoa. In the oögonia and ovarian follicle-cells in which I have been able to count the chromosomes, I have found but twenty-two; and the fact that none of these behaves in the characteristic manner of the accessory proclaims it the missing member.

We should expect therefore to find but one kind of mature ova in respect to number of chromosomes while we know that by the same standard there are two kinds of spermatozoa. Obviously, then, the number of chromosomes in the cleavage-nucleus of the fertilized egg (twenty-two or twenty-three) must depend upon the number introduced in the sperm-nucleus, since the latter contains either eleven or twelve, according as the accessory chromo-

some is absent or present. Now twenty-three is the number of chromosomes in the male cells, while twenty-two is the number I have found in the female cells, and thus we seem to find a confirmation of McClung's[1] suggestion that the accessory chromosome is in some way concerned in the determination of sex.

Without discussing here the logical consequences of such a conclusion, I will only emphasize the fact that one of the chromosomes, which in the primary spermatogonia[2] is scarcely distinguishable from its fellows, maintains throughout a long series of divisions an indubitable independence; and finally completely establishes its right to the title of a distinct individual by passing entire to one daughter-cell with the result that no accessory chromosome appears in the products of the next division of the other.

Taken as a whole, the evidence presented by the cells of *Brachystola* is such as to lend great weight to the conclusion that a chromosome may exist only by virtue of direct descent by longitudinal division from a preëxisting chromosome and that the members of the daughter group bear to one another the same respective relations as did those of the mother group — in other words, that the chromosome in *Brachystola* is a distinct morphological individual.

This conclusion inevitably raises the question whether there is also a physiological individuality, *i. e.*, whether the chromosomes represent respectively different series or groups of qualities or whether there are merely different-sized aggregations of the same material and, therefore, qualitatively alike.

On this question my observations do not furnish direct evidence. But it is *a priori* improbable that the constant morphological differences we have seen should exist except by virtue of more fundamental differences of which they are an expression; and, further, by the unequal distribution of the accessory chromosome we are enabled to compare the developmental possibilities of cells containing it with those of cells which do not. Granting the normal constitution of the female cells examined and the similarity of the reduction process in the two sexes, such a comparison

[1] McClung, C. E., "Notes in the Accessory Chromosome," *Anat. Anz.*, XX.; "The Accessory Chromosome, Sex-determinant," BIOL. BULL., III.

[2] A study of the chromosomes of the primary spermatogonia has been made in *Melanoplus differentialis*, a nearly related form in which the later divisions are essentially the same as in *Brachystola*.

must show that this particular chromosome does possess a power not inherent in any of the others — the power of impressing on the containing cell the stamp of maleness, in accordance with McClung's hypothesis.

The evidence advanced in the case of the ordinary chromosomes is obviously more in the nature of suggestion than of proof, but it is offered in this connection as a morphological complement to the beautiful experimental researches of Boveri[1] already referred to. In this paper Boveri shows how he has artificially accomplished for the various chromosomes of the sea-urchin, the same result that nature is constantly giving us in the case of the accessory chromosome of the Orthoptera. He has been able to produce and to study the development of blastomeres lacking certain of the chromosomes of the normal series.[2]

In larvæ resulting from double-fertilized eggs which have divided into three cells at the first cleavage, he recognizes an organism made up of definite thirds, each traceable to one of the original blastomeres and each characterized, as a result of the primary hap-hazard tripolar division, by a different combination and generally by a different number of chromosomes from that of its fellows. In rare instances such an embryo may be normal, of which fact the possibility that each pole of the triaster may receive a complete normal series of chromosomes is explanation enough. In other cases, the embryo may be completely normal (for instance in respect to skeleton or pigmentation) in one or two thirds, while in the remaining portion these structures may be entirely lacking; and it is a most significant fact that "in einzelnen dieser Fälle konnte aus der Kerngrösse nachgewiesen werden, dass die Grenze wo der Defekt beginnt, mit der Grenze zweier auf verschiedene Ausgangsblastomeren zurückführender Bereiche zusammenfällt." In the "normal" embryos mentioned above, every part was present, and as regards specific characters, normal; but in different thirds there could be seen individual variations which normally should have appeared in different larvæ. "In der

[1] Boveri, *l. c.*

[2] By the normal series is here meant such a one as occurs in the nucleus of either of the mature germinal products, since it has been clearly shown by the well-known work on the fertilization of enucleate egg-fragments and on chemically induced parthenogenesis, that either of the ripe germ-products possesses all the chromatin necessary for the production of a normal larva.

That," says Boveri, " könnte ich aus den verschiedenen Typen der normalen Kontrolzuchten, durch Kombination der rechten Hälfte einer Larve mit der linken einer anderen, Bilder herstellen, die den in Rede stehenden Dreierplutei fast genau entsprechen." To these points is added the fact that while all the isolated blastomeres of a normal four-cell stage develop exactly alike, those of dispermic three- or four-cell stages rarely or never do so, even when the numerical distribution of chromosomes appears equal; and, further, that in large numbers of larvæ from double-fertilized eggs all possible combinations of characters are to be found, just as all possible combinations of chromosomes from the three parent cells may enter into the composition of their nuclei. From these and other data, Boveri draws the conclusion that " Nicht eine bestimmte Zahl sondern eine bestimmte Kombination von Chromosomen zur normalen Entwicklung notwendig ist, und dieses bedeutet nichts anders als dass die einzeln Chromosomen verschiedenen Qualitäten besitzen müssen."

Thus we are brought to recognize a physiological individuality in a form in which the chromosomes are morphologically indistinguishable and the nuclei of which, after the anaphases, offer no mechanical hindrance to the free intermixture of the chromatin. We have already reviewed the reasons for believing the accessory chromosome in the cells of *Brachystola* to be the possessor of specific functions and it only remains again to call attention to the likelihood that the constant morphological differences between the ordinary chromosomes are the visible expression of physiological or qualitative differences.

In conclusion, from the point of view thus suggested, let us again consider the phenomena of fertilization. In either sperm- or egg-nucleus a complete series must be present since either may produce a normal embryo without the other. Every normal fertilized egg, therefore, as well as every cleavage-cell derived from it, must have the field of each character covered by two chromosomes — one from each parent. The chromosome series of the echinoderm cleavage-nucleus is thus shown to be physiologically a double one just as in *Brachystola* we have seen it to be morphologically double, and the doubling in both cases is seen to be accomplished in an exactly similar way — viz., by the contribution of equivalent series by the two parents.

If, as the facts in *Brachystola* so strongly suggest, the chromosomes are persistent individuals in the sense that each bears a genetic relation to one only of the previous generation, the probability must be accepted that each represents the same qualities as its parent element. A given relative size may therefore be taken as characteristic of the physical basis of a certain definite set of qualities. But each element of the chromosome series of the spermatozoon has a morphological counterpart in that of the mature egg and from this it follows that the two cover the same field in development. When the two copulate, therefore, in synapsis[1] the entire chromatin basis of a certain set of qualities inherited from the two parents is localized for the first and only time in a single continuous chromatin mass; and when in the second spermatocyte division, the two parts are again separated, one goes entire to each pole contributing to the daughter-cells the corresponding group of qualities from the paternal or the maternal stock as the case may be.

There is, therefore, in *Brachystola* no qualitative division of chromosomes but only a separation of the two members of a pair which, while coexisting in a single nucleus, may be regarded as jointly controlling certain restricted portions of the development of the individual. By the light of this conception we are enabled to see an explanation of that hitherto problematical process, synapsis, in the provision which it makes that the two chromosomes representing the same specific characters shall in no case enter the nucleus of a single spermatid or mature egg.

I may finally call attention to the probability that the association of paternal and maternal chromosomes in pairs and their subsequent separation during the reducing division as indicated above may constitute the physical basis of the Mendelian law of heredity. To this subject I hope soon to return in another place.

I take pleasure in expressing here my gratitude to Prof. E. B. Wilson for much valuable advice and assistance in the work upon *Brachystola* and in the preparation of the present paper.

ZOÖLOGICAL LABORATORY, COLUMBIA UNIVERSITY,
October 17, 1902.

[1] The suggestion that maternal chromosomes unite with paternal ones in synapsis was first made by Montgomery (1901, I.).

THE NERVOUS SYSTEM IN GONIONEMA MURBACHII.

IDA H. HYDE.

Some physiological work which I undertook this summer at the Woods Hole Biological Laboratory on the Hydromedusa, Gonionema Murbachii, made it important that I should know the distribution of its nervous system which at the time had not been described or known with certainty. I decided, therefore, to gain some knowledge of the distribution of its nerves by means of Bethe's methylene-blue method. Inasmuch as my time for this work at Woods Hole was very limited, I was unable to undertake an exhaustive histological study of the whole nervous system of the medusa. Believing it of some interest to make known the facts that were obtained, it was decided to publish them in a brief preliminary report, hoping in the near future to see the subject completed by Mr. Chas. G. Rogers who has consented to make a detailed histological study of the distribution of the nerves, in connection with some work which he is pursuing on regeneration in this animal, under the direction of Dr. Loeb.

All my observations were made on fresh material. The whole or small parts of the animal were exposed six or more hours to the action of a weak sea-water solution of Bx methylene blue freshly made and filtered for each study. The material was kept in a cool place and transferred for study from methylene blue to sea-water or a *m*/8 solution of sodium chloride. Some material was kept for future study as long as twenty-four hours on ice in 10 per cent. ammonium molybdate to which a few drops of 1 per cent. osmic acid and hydrogen peroxide had been added (1 gm. ammonium molybdate, 10 c.c. distilled water, 1 c.c. hydrogen peroxide, two drops 1 per cent. osmic acid).

Small pieces were dissected from different regions and examined with an oil immersion lens. The study of these sections disclosed, besides the double nerve ring around the margin; usually designated as the central nervous system, a third ill-defined very

narrow nervous strand, peripheral to the above, around the margin; a definitely outlined radial system along the radial canals, both below the epithelial cells of the subumbrella as well as deeper beyond the muscle layer, in the flat epithelial endo-

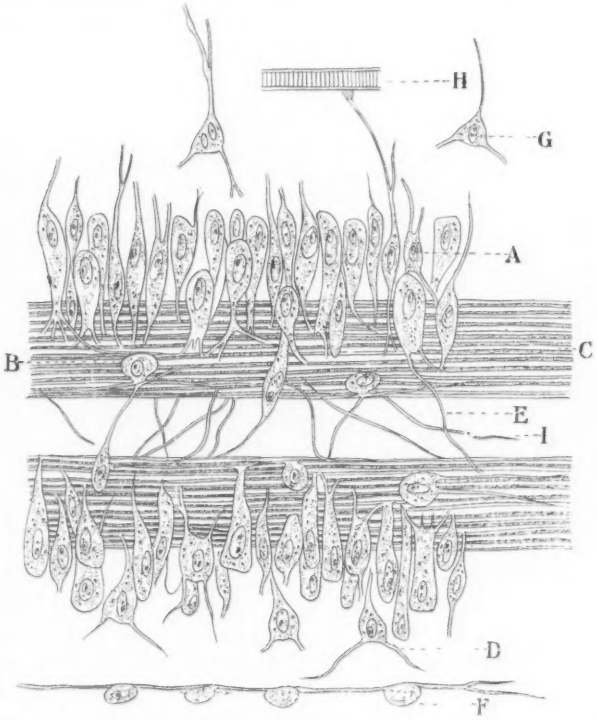

FIG. 1. Schematic view of a piece of the marginal nerve rings. Drawn from a study of many specimens studied with an oil immersion as well as lower power and camera lucida both from the sub- and exumbrella sides.

A, cells, transversely to the upper marginal ring.
B, ovoid cells with sheathed fibers.
C, nerve fibers parallel to the marginal ring.
D, multipolar cells proximal to the lower ring cells.
E, communicating fibers between the rings.
F, ovoid cells in the marginal strand.
G, multipolar cell of the subepithelial network.
H, muscle fiber.
I, space between upper and lower ring.

dermal layer; and a ganglionic and fibrous network beneath the epithelial layer of the subumbrella, which I believe sent nerve fibers beyond the endodermal flat epithelial-like cells, up to the gelatinous layer. The manubrium contains a ganglionic and fibrous network connected with large ganglia that lie along the radial area and smaller ones around its margin that send fibers to small sensory cells at its periphery, (Fig. 3).

A view from the exumbrella side of the margin of the animal discloses a narrow hyaline-like area between the marginal nerve rings (Fig. 1, *i*). It is along this line that the velum is attached. The upper nerve ring lies therefore above, the lower below the attachment of the velum. They are, however, not entirely distinct but are connected by communicating fibers that show most clearly, with proper focusing, from the subumbrella side (Fig. 1, *e*). The nerve rings are composed first of several rows of closely packed bi- and multipolar cells that lie tranversely to the nerve rings beneath the epithelial layer of the subumbrella (Fig. 1, *a*). They are very characteristic elongated cells with large nuclei. They usually taper at one end, more than at the other, and give off one or more fibers from the ends. Some of the fibers extend into the velum, some bend and run at a deeper level along with other nerve fibers around the margin, forming a double fibrous ring (Fig. 1, *c*). Some fibers extend into the other nerve ring, while still others extend toward the apex of the bell communicating either with the nervous network of the subumbrella, the radial nerves, or ending in muscle fibers. In addition to these snugly-packed spindle or ovoid-shaped cells, there are bipolar or multipolar cells, that lie at a deeper level in the fibrous portion of the ring canal (Fig. 1, *b*). The fibers emerge from the same side of the bulging or ovoid cells and extend in opposite directions among the fibers of the nerve ring (Fig. 1, *b*). At close intervals and proximal to the transversely situated cells of the lower marginal ring are, moreover, large multipolar cells that send fibers toward the periphery of the margin as well as into the nerve ring. A row of flattened ovoid bipolar cells form a third nerve ring of fibers and cells peripheral to those described above (Fig. 1, *f*). Pieces of tissue dissected from the umbrella in the region of the radial canals and exam-

ined both before and after removal of the genital glands, the cœlenteric canal or overlying gelatinous layer, show from the subumbrella side, at the border of the radial canal, closely arranged bi- and multipolar cells (Fig. 2, *k*, *j*) and focusing a little deeper a band of fine parallel nerve fibers intermingled with ovoid nerve cells that send off thicker fibers (Fig. 2, *j*, *l*). Focusing still

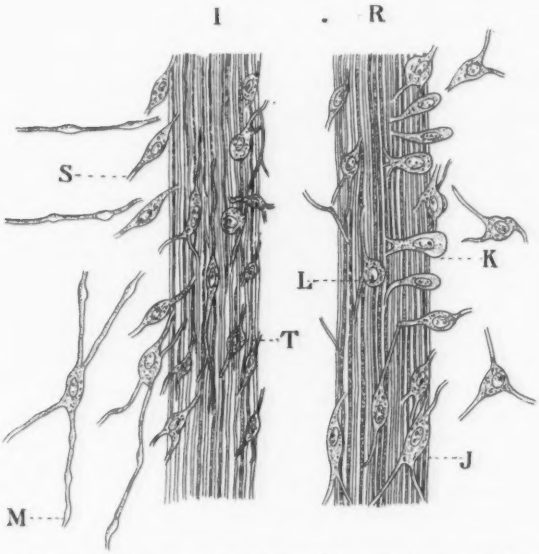

FIG. 2. Schematic view of a piece of the radial nerve tissue. The band at the right (*R*) represents the nerve cells below the ectodermal epithelium of the subumbrella; at the left (*I*) those between the muscles and the endodermal cells as seen from the exumbrella side.

J, multipolar cells, close to radial nerve fibers.
K, radial tissue cells.
L, ovoid cells among the radial nerve fibers.
M, beaded fiber of subepithelial network.

deeper, beyond the radial muscle fibers, somewhat smaller bi- and multipolar cells come to view (Fig. 2, *s*, *t*). The latter can best be seen from the exumbrella side. The first kind of cells lie below the ectodermal epithelium of the subumbrella. Some of their fibers extend laterally, seemingly to the muscles or the subumbrella network of ganglia and fibers (Fig. 2, *j*), others

go to the band of parallel nerve fibers and the nerve ring. These cells are more numerous in the neighborhood of the latter. Studied from the exumbrella side it was seen that the parallel nerve fibers lay close to the radial muscle fibers, and that besides the bi- and multipolar cells beneath the ectodermal epithelium, there were other, smaller, bi- and multipolar cells, situated between the muscle layer and the endodermal epithelium.

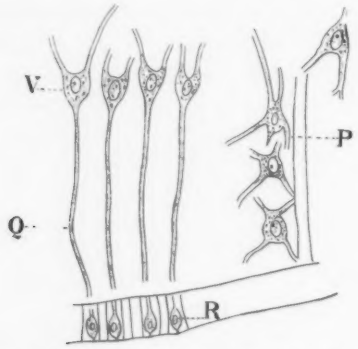

FIG. 3. Schematic view of nerve cells in a piece of the manubrium from its margin in the radial region.

P, multipolar cells in radial region of manubrium.
Q, fibers from multipolar cells at border of manubrium.
R, sensory cells in epithelium of manubrium.
V, multipolar cells at the border of manubrium.

The fibers from these cells seem to go to the genital glands, the cœlenteric canal and narrow band of muscle fibers beneath the radial cœlenteric canal, as well as into the parallel layer of nerve fibers. It may be that these are especially concerned with the digestive and reproductive systems.

In addition, therefore, to the marginal nerve ring and the radial nervous system, there is the peripheral network of cells and fibers that exist beneath the epithelium of the subumbrella. The cells of this network are triangular and multipolar with sheathed fibers that have slight thickenings at different places in their extent. Some lie close to the radial (Fig. 2, *m*), others to the marginal nerve bands (Fig. 1, *g*). Then, too, in a line midway be-

tween the radial nerves, the cells lie radially closer, sending some of their fibers up to the gelatinous layer. This net-work thus serves as a connecting link between the radial and marginal nervous structures. The manubrium also has its network of cells and fibers and along the margin of the manubrium is a row of large multipolar cells (Fig. 3, *v*) that send fibers to the periphery where they join special sensory cells that lie among the epithelial cells (Fig. 3, *r*). In the radial region of the manubrium are larger closely set nerve cells. It was seen that fibers from the nerve rings extend to the tentacles and sense organs, and that the latter contained most peculiar nerve tissue. To understand that and the endings of the different nerve fibers, requires detailed histological study of sections of the various regions of the body. This I hope will be done in the near future.